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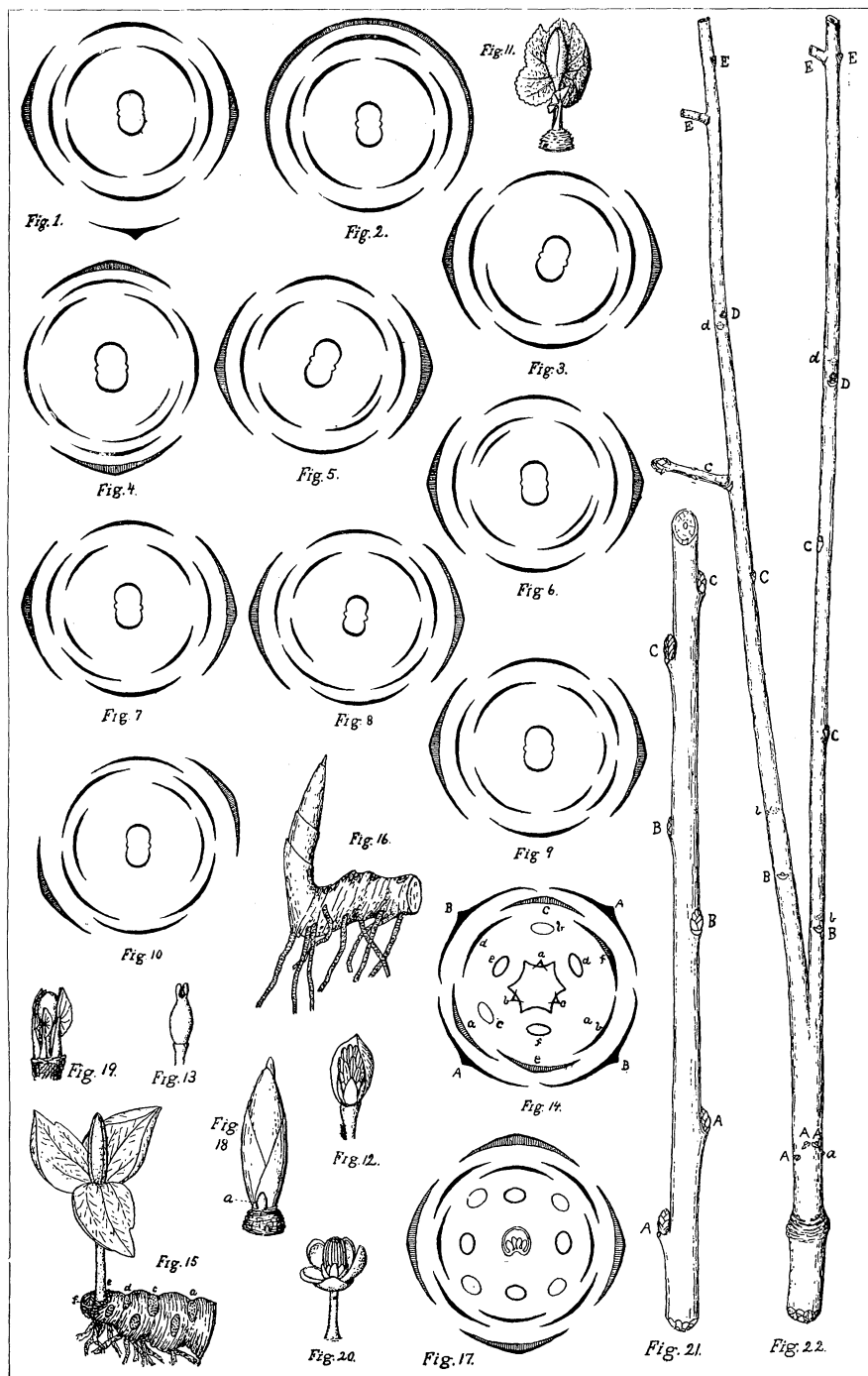
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**Abnormal phyllotactic conditions as shown by the leaves
or flowers of certain plants.**

AUG. F. FOERSTE.

(WITH PLATE XIV.)

Sanguinaria Canadensis.—Baillon interpreted the flowers of the blood-root so as to make the petals form two decussating dimerous whorls, which by dedoublement have become whorls of four petals each. The petals of the inner whorl should therefore be directly superposed to those of the outer whorl, and the two sepals should occupy a position intermediate between two petals of the outer whorl in each case. Eichler, in his important work "Blüthendiagramme," copies this view. Unfortunately this interpretation is incorrect, as may be seen at any locality where the blood-root is at all common. For the purpose of the following notes many hundreds of flowers were examined, and the accompanying diagrams illustrate all the cases found.

It is not a rare occurrence in some, perhaps isolated, localities to find a single scale about half way up the flower peduncle, subtending a second flower. In this case the sepals of the subtended flower seem to occupy a position transverse to that of the scale. The outer set of four petals is interpreted as consisting of two dimerous whorls, the lower pair of petals decussating with the sepals, and the other pair of petals taking a position directly above the sepals. The inner set of four petals alternates with the outer set taken as a whole, and may be interpreted either as a dimerous whorl decussating with the second pair of petals, and numbering four in consequence of dedoublement, or as a whorl of four petals, showing the usual arrangement of whorls consisting of four members preceding or following dimerous whorls. The latter interpretation is shown to be the correct one by such cases as are represented by fig. 3, in which the inner whorl of petals is reduced to three, but the odd petal never occupies a median position above one of the outer petals, as it should if it represented the undivided petal of a dimerous whorl. The pistil consists of two leaves, which typically decussate with

the sepals, so that the position of the sepals can be determined even when they have fallen off, which they do as soon as the flower opens. This typical arrangement of the flowers is illustrated in fig. 1. The stamens have been omitted from this diagram because nothing definite could be determined regarding their arrangement. However, the fact that the leaves forming the pistil decussate with the sepals suggested the following interpretation. The stamens are too numerous to be interpreted as a single whorl, even if dedoublement be allowed its play, especially when it is considered that *Canbya*, showing the smallest number of stamens known, six, possesses at least two whorls of stamens, and that most species demand a greater number. The blood-root must have more than two whorls in order to make the pistil leaves decussate in regular succession with the previous whorl, and with the sepals. Three whorls at least are therefore represented by the stamens, but for the present all question of dedoublement must be left undecided.

During the examination of a great number of flowers belonging to the same species it was to be expected that anomalous forms would be found. Most of these were isolated cases, such as a single sepal, evidently formed by the junction of the two ordinary sepals, fig. 2; or the more important case of sepals occupying a position directly beneath the pistil leaves, fig. 4, in which case it is necessary to assume an even instead of an odd number of staminal whorls in order to explain away their abnormal position, or rather the abnormal position of the pistil leaves. Slightly diagonal positions of the sepals are occasionally met with, but the extreme cases, such as that illustrated in fig. 10, are almost always more apparent than real, and rest upon the fact that the attachment of the sepals at their base takes up about half of the circumference of the peduncle at this point. As this base, however, represents the linear area from which the development of the sepals proceeded, a slight extension of this area to the right or the left often serves to place the indefinite median line of the sepals in a position more or less oblique to the remaining members of the flower. These exceptional conditions are mentioned only for the sake of completeness.

A far more interesting group of variations from the typical arrangement first described is that shown by the petals, and when the great frequency of such variations from the type is

considered, the fact that they can all be reduced to a few series is extremely interesting. It is especially to be noted that the abnormal conditions immediately to be cited, regarding the arrangement of the petals, have no subsequent effect upon the position of the pistil leaves, and therefore can not consist in the interpolation of new whorls of petals, but must arise from dedoublement and the new conditions which dedoublement in preceding whorls often forces upon those which immediately succeed. The most common case consists in the addition of one, figs. 4 and 5, or two petals, fig. 6, to the inner whorl of petals, in such a manner that they take a diagonal position in the flower diagram, more or less approaching the transverse position which a dimerous whorl should take if it were added to the whorls already existing. That these petals are not to be interpreted in this way, but as formed by dedoublement in the nearest petals, is suggested by the unchanged position of the pistil leaves, as already mentioned. A second case consists in the removal of one, fig. 7, or two petals, fig. 8, belonging to the inner whorl of four petals, to the middle dimerous whorl, thus giving the second whorl of petals three or four members instead of two. Since this removal takes place in a direction away from a transverse line connecting the sepals the result is to leave the original petals in nearly their normal position, and to bring the added petals into a median position. That this second whorl does not consist typically of four petals in these cases is shown by the fact that the space opposite the intercalated petals is left vacant, whereas a whorl of four members should be equally distributed. According as one or two petals have been removed from the inner whorl to the middle whorl, one or two petals are added to those remaining in the inner whorl and these added petals are again placed near a transverse line connecting the sepals, but on the same side of this line.

In a third case, one, fig. 9, or both petals of the second dimerous whorl have become two by dedoublement. In that case the four petals of the inner whorl occupy as nearly as may be their original positions and one, fig. 9, or two petals are added to their number and then occupy the interval created by the separation of petals of the second whorl into two through dedoublement. In this case the addition is made precisely in line with the transverse position occupied by the sepals. The three variations from the type just described are

all frequent enough to be considered characteristic of this plant. The first variation is the most common, the second, next, the third, least frequent.

A unique case is illustrated in fig. 10. Here the oblique position of the sepals is not considered of moment owing to the normal position shown by the first set of petals; it is illustrated, however, because it is the only *good* case of oblique position of sepals found during these investigations. The second set of petals consists of four members. It would be easy to say that dedoublement had taken place but then in that case two of the petals of the inner whorl should not take up a position so decidedly transverse to that shown by the first whorl of petals. Again the interpretation of the inner whorl as a dimerous whorl is excluded by the third petal which seems to make an effort to continue the greater number of members usually shown by this whorl. If this case were not unique, it would spoil all value of the previous observations.

As it is, a number of interesting facts seem to have been brought to light, not usually considered in the study of phyllotactic arrangements shown by flowers. The first of these is that new members are not added indifferently to those already existing, but follow certain laws or tendencies. The most general of these, in the blood-root, is that added members have a tendency toward placing themselves in a position more or less in line with the sepals, obliquely so in the first set of variations described, on one side of this line in the second set, and exactly in line in the third set. These positions are more or less approximately that which a new dimerous whorl would take if added to those already existing. A second fact is that succeeding whorls attempt to accommodate themselves to abnormal conditions shown by previous whorls. This finds its best expression in the intercalation of new petals in succeeding whorls in order to fill up the interval caused, apparently by dedoublement, in the preceding whorl. A third fact is that these changes in the arrangement of the petals as here instanced have taken place without producing any effect upon the position of the leaves of the pistil, and hence have not the value of newly added whorls. It is difficult to decide how far dedoublement can account for these phenomena, where its application has been quoted, or even omitted.

The slightly oblique position shown occasionally by the pistil leaves, is due largely to crowding during their later development in the bud.

The buds should be studied at as early a stage as possible. Fig. 11 represents a plant, as it was seen on Feb. 15th, during a very cold winter. The protecting scales have been removed and the larger leaf forcibly expanded. Fig. 12 shows the petals and stamens, partly enclosed by one sepal, the other having been cut away. Fig. 13 gives a slightly magnified view of the pistil at this period. It is evident from the size already attained by the organs, that flower buds should be studied for phyllotactic purposes during the summer previous to their flowering season.

Trillium sessile.—In the spring of 1882 a four leaved *Trillium* was found which illustrated admirably the attempt of succeeding whorls to continue or accommodate themselves to the abnormal conditions presented by previous whorls. This case is illustrated by fig. 14; the letters serve to designate the flower members but have no other significance. In the normal development of this plant there should be three sepals and three petals, in decussating whorls. The outer set of floral envelopes, marked *a*, *b*, *c*, should have been sepals, and the inner set, marked *d*, *e*, *f*, should have been petals. Instead of that, sepal *e* occupies the position of a petal, and together with sepal *c* attempts to attach itself to the whorl of four leaves as though it were an independent dimerous whorl of sepals. This attempt, however, is spoiled by sepal *a* in its usual position, but as if to maintain at least the semblance of a dimerous whorl, that part of petal *f* which lies next to sepal *c* is colored greenish like a sepal, and thus *c* and half of *f* are opposed to *a* and *e*. Further *b*, which should be a sepal, is developed as a petal, and only two of the first whorl of stamens are in existence, *b* and *c*, the third *a* being entirely absent. The second whorl of stamens and the leaves present the normal conditions. If now this case be considered as the attempt of a trimerous plant to accommodate itself to the dimerous conditions presented by the leaves, then the absence of a stamen in the first whorl can be explained. The dimerous whorl of leaves *A*, *A*, is succeeded in decussating order by a second similar whorl *B*, *B*; and this in a similar way by *a*, *e* and *c* with the adjacent part of *f*, all acting together as a simple dimerous whorl, decussating with *B*, *B*, and all having a greenish color. With this in turn the purple petals *d* and *b* are found decussating, occupying a position almost directly in line with the leaves, *B*, *B*. The trimerous character of the plant

retains sufficient power to keep half of *f* deep purple as a petal should be. Decussating with *d* and *b* are the stamens *b* and *c* as a dimerous whorl. The stamen *a* which is absent, would be out of place in a dimerous whorl. The typical trimerous character is first again fully developed in the second set of stamens and is retained by the pistil leaves.

The appearance of this plant in early winter is shown by fig. 16. The seedling always starts to grow near the surface of the ground, and pushes its way laterally under the soil. Fresh roots start each year from the anterior growths of the stem, the older roots decay, and when with age the anterior roots begin to wrinkle and hence to contract, they have a tendency to pull the growing end of the *Trillium* deeper and deeper into the soil. In a similar way the roots of *Symplocarpus foetidus* and *Arisæma triphyllum* draw the stems or corms of these plants deeper and deeper into the soil, but in the latter cases directly downwards. Fig. 15 shows the leaves and flower bud of fig. 16, with the protecting scales removed. At the base of the flowering stem *e* is seen a bud *f*, which represents the flowering stem of the season following *e*. The rootstock has been wrenched so as to show better the fact that the flowering stems and hence their scars *d*, *c*, *a*, and others are placed alternately on the right and on the left side of the rootstock.

Jeffersonia diphylla.—Gray has given a diagram for the flowers of the twin-leaf which makes them tetramerous, with the exception of the pistil which has only one leaf. (Genera Fl. Amer. Bor. Ill., vol. i, 34). In southwestern Ohio, where this plant is very abundant, the calyx almost always has five members, arranged rather on the plan of a spiral than that of a whorl. Four sepals were a comparatively rare exception. Two whorls of petals and two whorls of stamens were tetramerous in either case, whether the sepals were four or five in number. Typical Berberidaceæ possess an equal number of members in each of the whorls of the sepals, petals, and stamens. Perhaps it was the attempt to correlate the diagram of *Jeffersonia* with those of typical Berberidaceæ which led to the selection of the less frequent forms with a tetramerous calyx, as representing the typical *Jeffersonia*. The rarity of tetramerous forms in the calyx, and the frequency of flowers with five sepals however, makes it plausible that the five-sepaled calyx still points to the original pentamerous spiral

character of these whorls, which at present is no longer shown by the petals and stamens. In fig. 17, the figure given by Gray is repeated with certain variations, in order to call attention to the peculiar position of the single pistil-leaf. This leaf should fall opposite one of the stamens of the outer whorl. As a matter of fact, however, it is opposed to a stamen belonging to the inner whorl in the flowers examined.

Fig. 18 represents a subterranean bud of the twin-leaf, collected Feb. 15th with a few scales removed in order to show, at *a*, the bud from which is to develop the flowering bud two years hence. Fig. 19 shows the same bud after the removal of all the scales, in order to show the flower bud of the next season, surrounded by the leaves of the same season. Fig. 20 presents a view of this flower bud after the petals have been forcibly spread apart, showing the petals and stamens.

Rhamnus lanceolatus.—The branches of many shrubs near Dayton, Ohio, showed the leaf arrangement indicated in fig. 21, which may be briefly characterized as consisting of decussating dimerous whorls of leaves, in which the leaves, apparently belonging to the same node, are not strictly opposite to each other, but are separated by a more or less pronounced interval. This interval is in most cases not large enough to altogether destroy the effect of decussating whorls as just described. The same plants often show a typical two-fifths phyllotaxy. As a rule species of *Rhamnus* are described as possessing an alternate arrangement of leaves.

Fraxinus.—A twig collected at Granville, Ohio, is represented by fig. 22, but only one-fourth of its natural size. Here a branch has divided dichotomously, between the nodes *A* and *B*, but that the dichotomous character was already developed at a much earlier period is shown by the development of four leaves at the node *A*; the median two leaves should have met at the centre of the compound stem at this locality, but they have been crowded towards the exterior so that both appear in the figure here presented. That the dichotomous character was developed at an even earlier stage is shown by the position of the upper scales of the winter bud. The effect of this irregularity (best seen at *A*, upon the succeeding nodes *B*, and *C*,) is to increase the interval between the leaves belonging to the same node, already shown at *A*. This interval again diminishes at the node *D*, and ceases at node *E* in one branch and at node *F* (not figured) in the

other. The lateral branches are all normal. This case is quite typical for phenomena as shown by dichotomously branching abnormal stems with opposite leaves. The small letters indicate that the leaves are situated on the side of the branch away from the observer, and these leaves are indicated by dotted contours in the figures.

Heidelberg, Germany.

A study of some anatomical characters of North American Gramineæ. I.

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The genus *Uniola*.

(WITH PLATE XV.)

In the year 1810, when Brisseau-Mirbel said:¹ “Le seul moyen de perfectionner les familles naturelles, est à joindre à l'étude des caractères botaniques, celle de tous les faits relatifs à l'anatomie et à la physiologie,” he hardly thought of the important change that would come about in systematic botany. The rapid increase in the number of species known made it evident that botanists must not content themselves with the mere external characters, but that others should be sought. Later appeared a series of researches especially by French and German authors, wherein an attempt was made to give anatomical diagnoses to a number of species; most successfully by Duval-Jouve, Radlkofer and Vesque. The importance of studies of that kind was very clear; they not only furnished additional and often even more reliable systematic characters, but they extended the study of anatomy into wider fields than ever before, until anatomy has become one of the most important modern lines of botanical science.

And the study of internal structure gave also a most striking illustration of the physiological life; it became easy to infer from the structure the conditions under which the plant had lived, whether in dry or moist localities, exposed to the sun or in deep shade, etc. Anatomy also rendered great help in the discrimination of species, as shown for instance by

¹ Sur l'anatomie et la physiologie des plantes de la famille des Labiées. (Ann. du Muséum d'Hist. Nat. vol. xv.)